8 Implications of Increasing Carbon Dioxide and Climate Change for Agricultural Productivity and Water Resources

J. Goudriaan

Agricultural University
Wageningen, the Netherlands

M. H. Unsworth

University of Nottingham
Loughborough, United Kingdom

ABSTRACT

Green plants need CO_2 to grow. A higher concentration of atmospheric CO_2 will stimulate the photosynthetic process, promoting plant growth and agricultural productivity without increasing the water demand for crop transpiration. On the other hand, expected climatic warming may have adverse effects on agriculture, partly offsetting the positive direct CO_2 effects. The availability of water resources depends on precipitation and potential evaporation, but also on many other factors. Interannual variability cannot be used to extract information of the impact of gradual climatic change. About 5 to 10% of the actual rate of increase of agricultural productivity worldwide can be ascribed to the fertilizing effect of rising atmospheric CO_2. The positive direct effect of CO_2 on plant growth is often smaller when crops are poorly fertilized, but it is fully retained when water shortage limits productivity. Beneficial and detrimental effects of climatic change will not be evenly distributed over the world. Cool and temperate climatic zones will benefit, but in the tropics a further increase in temperature will be undesirable. These changes will exert their influence at such a slow rate that they will be hardly noticeable compared with changes in technology and in economy. Yet they will gradually affect the range of options available.

CLIMATIC EFFECTS

Several atmospheric trace gases such as CO_2, CH_4, and N_2O influence the Earth's climate by transmitting incoming solar radiation, while partly blocking outgoing terrestrial black-body radiation. As the concentrations of

 Impact of Carbon Dioxide, Trace Gases, and Climate Change on Global Agriculture, ASA Special Publication no. 53.

these so-called greenhouse gases rise, less terrestrial radiant energy can escape through the Earth's atmosphere. Global surface temperature will rise and restore the radiation balance of the Earth, but a series of interrelated processes that may enhance or reduce this primary effect make it very difficult to predict the final outcome. For example, one important positive feedback process acts by increasing the concentration of water vapor, which itself has a greenhouse effect. On the other hand, a negative feedback may occur through stronger cloud formation (Ramanathan et al., 1989).

The best available estimates now, based on general circulation models, GCM's, predict a global average of 2.5 to 5.5 °K temperature increase, accompanied by some 5 to 15% increase of the circulation rate of the hydrological cycle (Taylor & MacCracken, Chapter 1, this book; Wilson & Mitchell, 1987). We shall briefly review the direct effects of CO_2 and climatic variables on plants and then consider the implications for global agricultural productivity and water resources. Parry et al. (1988) reviewed the subject more broadly.

DIRECT PHYSIOLOGICAL EFFECTS

The trace gas CO_2 is the primary source of C for plant growth. Its present natural concentration is often suboptimal, and for this reason CO_2 enrichment is widely employed in glasshouses to raise yields of crops such as tomato (*Lycopersicon esculentum* Mill.), lettuce (*Lactuca sativa* L.), cucumber (*Cucumis sativus* L.), and flowers (Wittwer & Robb, 1964; Enoch & Kimball, 1986; Nederhoff & van Uffelen, 1988).

The major physiological effect of increased CO_2 is to increase the rate of CO_2 assimilation. Generally, the utilization efficiency of other plant growth factors (e.g., radiation, water, nutrients) is also improved. These direct physiological effects are considered by Acock (Chapter 4, this book) and by Idso (Chapter 5, this book). A large body of research in this field was brought together in the thorough review edited by Strain and Cure (1985) for the U.S. Department of Energy. Likewise, reports have been prepared in the Netherlands (Gezondheidsraad, 1983, 1987) and in Great Britain (Squire & Unsworth, 1988). For this reason we can permit ourselves to be brief, but for clarity some repetition cannot be avoided.

Interactions and partial compensations of direct and indirect effects may occur. The results of some crop growth models that allow for these compensations will be discussed.

DIRECT CARBON DIOXIDE EFFECTS ON LEAF, CANOPY, AND CROP

Leaf Response of Photosynthesis

A large body of evidence is available on experimentally established effects of ambient CO_2 (C_a) on the photosynthesis of leaves and crop canopies, and

on the subsequent dry matter accumulation in several crop components (Lemon, 1983; Strain & Cure, 1985; Kimball, 1983; Cure & Acock, 1986; Acock, Chapter 4, this book). Light is indispensable for the process of photosynthetically driven CO_2 uptake by green plants. In the natural environment, light and CO_2 are normally suboptimally present; consequently, photosynthesis is stimulated by an increase of ambient CO_2 (Fig. 8-1), not only under high light, but also under low light conditions.

There are two major classes of plants called C_3 and C_4 plants, which differ in biochemical and anatomical aspects of the way they take up CO_2 from the ambient air (see Acock, Chapter 4, this book). In C_3 plants the enzyme that binds CO_2 with RuBP, can also bind RuBP with O_2, after which RuBP must be recovered (Farquhar & von Caemmerer, 1983). This recovery costs energy and releases CO_2, observable as photorespiration. Because CO_2 and O_2 compete for the same site on the catalyzing enzyme, photorespiration is suppressed by higher CO_2. In the other direction, when CO_2 is lowered to the level where CO_2 uptake and CO_2 release just balance each other, this concentration is called the CO_2 compensation point, Γ (Fig. 8-2). The value of Γ is about 50 μmol mol^{-1} at 25 °C and rises with increasing temperature. The level of Γ is proportional with O_2 concentration. The light-saturated rate of photosynthesis is proportional to ($[CO_2] - \Gamma$) up to

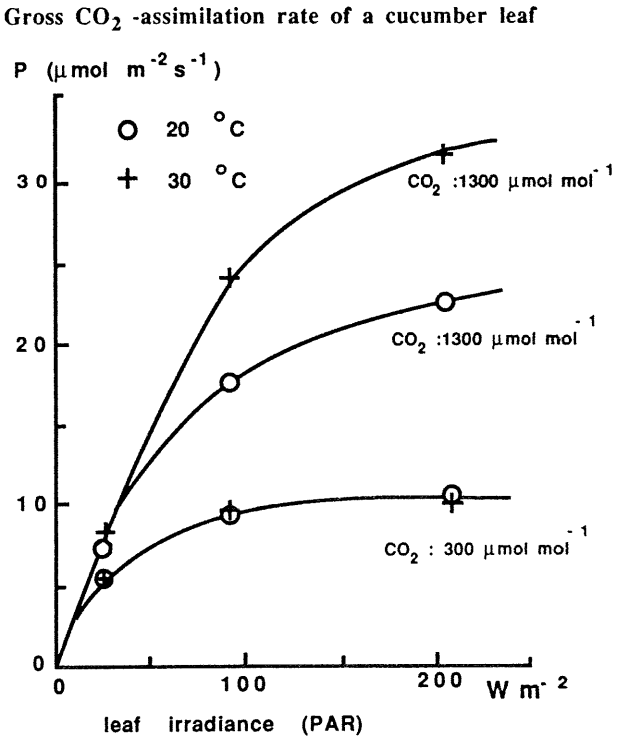

Fig. 8-1. Typical photosynthesis–light response curves, as stimulated by higher CO_2 (after Gaastra, 1962).

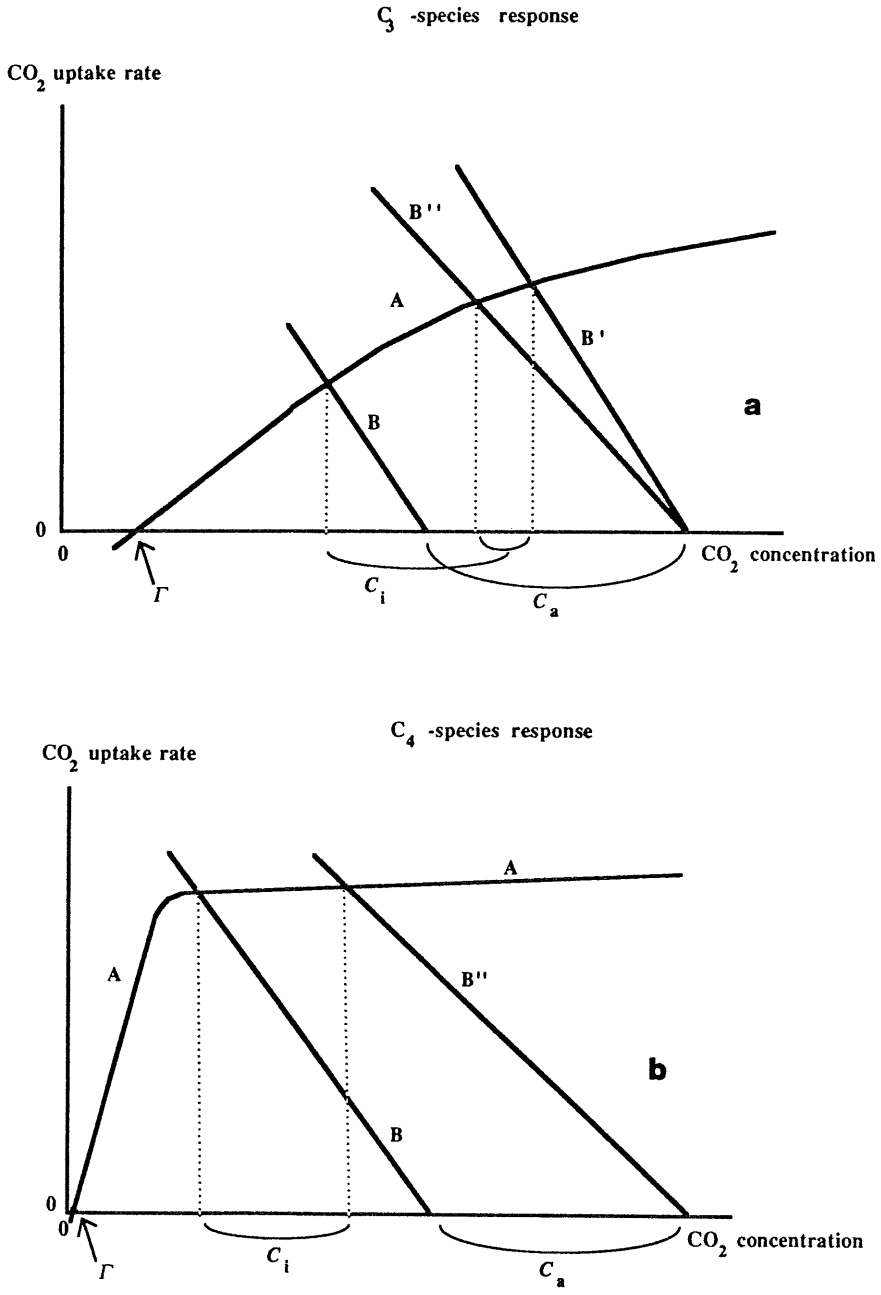

Fig. 8-2. Response (line A) of leaf photosynthesis to CO_2 inside the stomatal cavity (C_i). The rate of photosynthesis also affects C_i due to stomatal supply limitation (line B). Lines B′ and B′′ are for doubled CO_2, with B′ for no stomatal response and B′′ for partial stomatal closure due to the doubled CO_2, respectively. (See also Pearcy & Ehleringer, 1984). (*a*) a C_3 plant (strong assimilation response to CO_2; (*b*) a C_4 plant (only assimilation response to CO_2 at low concentration).

a concentration of about 1000 μmol mol^{-1}, and the initial light use efficiency increases with CO_2 in proportion with $([CO_2] - \Gamma)/([CO_2] + 2\Gamma)$ (Goudriaan et al., 1985).

In C_4 plants {mostly tall tropical grasses such as millet (*Panicum miliaceum* L.), maize (*Zea mays* L.), sorghum [*Sorghum bicolor* (L.) Moench] and sugarcane (*Saccharum officinarum* L.)} not RuBP but PEP, which does not bind with O_2, is used as a preliminary binder of CO_2 from the external air. The bound CO_2 is transported from the mesophyll cells to the sheath bundle cells in the form of organic acids and then released. The RuBP-CO_2 reaction is concentrated in these bundle sheath cells, where a very high CO_2 concentration is maintained. Oxygen gets practically no chance to bind with RuBP, so that photorespiration is suppressed and Γ stays low (about 5 μmol mol^{-1}). Because of the high affinity of PEP to CO_2, the photosynthetic response to CO_2 is very steep until about 100 μmol mol^{-1}. In the normal range of CO_2 of 300 to 500 μmol mol^{-1}, the C_4 leaf assimilation rate rises only little with CO_2, even under high light intensities.

Leaf Response of Stomatal Conductance

A typical secondary effect of raising C_a is partial stomatal closure, which increases the exchange resistance between leaf and ambient air to gases such as CO_2 itself and water vapor (Raschke, 1975; Morison, 1987). The presence of stomatal pores in the epidermis of leaves permits uptake of CO_2 from the ambient air, but at the same time water vapor escapes, leading to transpiration. The degree of opening can be considered as a compromise in the balance between limitation of water loss and admission of CO_2. The generally observed strong correlation between stomatal conductance and demand for CO_2 is an expression of this compromise (Wong et al., 1979).

Not only is stomatal conductance well correlated with photosynthesis when light varies (Goudriaan & van Laar, 1978), but also when unfavorable conditions occur such as air pollution, shortages of water or nutrients (Goudriaan & van Keulen, 1979), or senescence (Goudriaan & van Laar, 1978). The much higher affinity for CO_2 in C_4 plants permits them to maintain a more favorable ratio between net CO_2 uptake and stomatal conductance. Typically the concentration ratio of intercellular CO_2 (C_i) to ambient CO_2 is about one-third in C_4 plants, but about two-thirds in C_3 plants.

When ambient CO_2 is raised, net CO_2 assimilation may be increased and/or water loss may be reduced, depending on how the stomata react. In Fig. 8-2 the supply-demand function of assimilation and CO_2 is given. The figure shows how the assimilation rate responds to intercellular CO_2 concentration (line A). The intercellular concentration declines from C_a linearly when assimilation rate increases (line B), due to the resistance offered by the stomata and leaf boundary layer. The intersect of the two lines (line B with line A) gives the realized rate of assimilation and of intercellular CO_2 concentration. Raising external CO_2 will cause a maximal assimilation effect (line B ′) if stomata do not respond at all, but usually the stomata close somewhat (line B ′ ′). In the extreme situation of constant intercellular CO_2

the stomatal effect will be maximal, but the assimilation effect will have vanished. The most common response is that the ratio of intercellular to external CO_2 concentration is stabilized, thereby partitioning the effect between assimilation and water loss. This constant C_i/C_a ratio means that stomatal aperture is reduced very little if assimilation responds strongly to C_i (typical in C_3 plants). In C_4 plants photosynthesis uptake is usually almost CO_2 saturated, and stomatal closure is maximal (Fig. 8-2b).

A compilation of data by Morison (1987) showed that stomatal conductance at $C_a \approx 660$ μmol mol^{-1} was reduced to about 60% on average compared with the value at 330 μmol mol^{-1}. The variability around this reduction resulting from varying responses of assimilation to doubled CO_2, ranging from none in C_4 plants to about 40% in C_3 plants, is not large. In both groups water use efficiency (WUE) is considerably stimulated by increased ambient CO_2, either by stimulated assimilation rate or by reduced transpiration rate. Typically in C_3 plants transpiration will be reduced by 10 to 20% and assimilation stimulated by 40%, and in C_4 plants only transpiration will be reduced, up to about 25%.

Canopy Response

Leaf responses as described above are also found in well-ventilated canopies (Fig. 8-3, after Louwerse, 1980).

Doubt has been raised (Jarvis & McNaughton, 1986) about whether a CO_2-induced reduction of transpiration can be maintained on the scale of

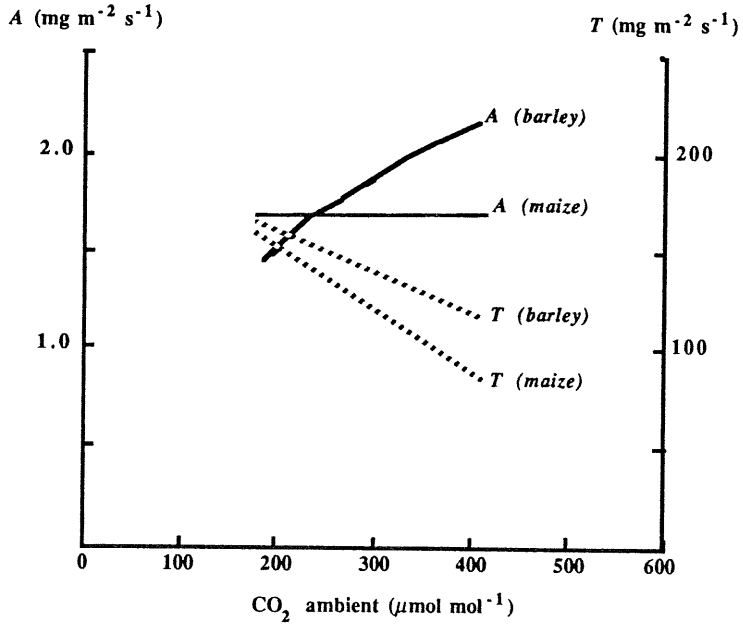

Fig. 8-3. Measured canopy responses to ambient CO_2 of photosynthesis (A) and transpiration (T) in barley (*Hordeum vulgare* L.) (C_3) and maize (C_4) (after Louwerse, 1980).

extended vegetated surfaces, because negative feedback by increased leaf-air humidity gradients may nullify the initial gain. Such a negative feedback will be particularly strong when there is a poor coupling with the atmosphere in conditions of low wind and/or an aerodynamically smooth crop surface.

This is, however, only part of the story. Precisely in those circumstances of large boundary layer resistance, the canopy air tends to be depleted in CO_2. Increased atmospheric CO_2 will then be effective in removing this depletion limitation and in stimulating assimilation rate. As a result, although transpiration will be reduced less, assimilation will be stimulated more than initially expected.

Microweather simulation enables an investigation of these effects on a canopy scale. Rosenberg et al. (1990) calculated that a 40% increase in stomatal resistance reduced evapotranspiration between 9% [in wheat (*Triticum aestivum* L.)] and 18% (in grassland), which shows that the effect of stomatal resistance is considerably reduced but not nullified.

In this chapter, results are presented from a stratified micrometeorological model (Goudriaan, 1977; Chen, 1984), which also included CO_2 effects on photosynthesis (Goudriaan et al., 1985). This model includes detailed in-canopy profiles of radiation and of aerial conditions, using first-order turbulent transport theory. The leaf energy balance and soil surface energy balance are based on the Penman-Monteith combination equation. Exchange above the canopy is modelled according to similarity for wind, mass, and heat, corrected for thermal gradients.

The results (Table 8-1) showed that in the more realistic simulation (Case b), the reduction of transpiration by doubled CO_2 was less than in the oversimplified run (Case a), where the micrometeorological feedback was ignored. Interestingly, the micrometeorological feedback enhanced the positive CO_2 effect on assimilation. This simulation included almost all steps in the scaling-

Table 8-1. Simulated effects of doubled CO_2 on daily assimilation (A), on daily transpiration (T), and on water use efficiency (WUE) for C_4 and C_3 plants, calculated by the Goudriaan-Chen model. In the control situation, crop height was 0.2 m and leaf area index was fixed at 4.

	C_4			C_3		
$[CO_2]$	A	T	WUE	A	T	WUE
μmol mol^{-1}	g m^{-2} d^{-1}	kg m^{-2} d^{-1}	g kg^{-1}	g m^{-2} d^{-1}	kg m^{-2} d^{-1}	g kg^{-1}
A. With air conditions defined at a height of 0.2 m (no micrometeorological feedback)						
350	88.03	3.516	25.04	63.988	4.562	14.03
700	88.03	2.265	38.87	96.477	3.729	25.87
Ratio	1	0.644	1.55	1.508	0.817	1.84
B. With air conditions defined at a height of 20 m (so that there was micrometeorological feedback)						
350	88.03	3.631	24.24	61.03	4.074	14.98
770	88.03	2.699	32.62	94.39	3.654	25.83
Ratio	1	0.743	1.35	1.547	0.897	1.72

up process mentioned by Jarvis and McNaughton (1986). Only the step from large field to region was not included.

In C_4 species, the simulated assimilation rate was not affected, but the stomatal resistance was almost proportional to external CO_2. Indeed, the simulated crop resistance around 1200 h (noon) increased from 70 to 127 s m^{-1}, which is a reduction to 55% in terms of crop conductance. The transpiration rate, however, did not decrease in the same proportion: it was reduced to 64% when microclimatic air conditions inside the canopy were kept the same. This stabilization of transpiration rate was caused by increased leaf temperature. When not only leaf temperature, but also the microclimatic air conditions inside the canopy were affected, transpiration crept up further to reach 74% of the original value.

For C_3 species the major CO_2 effect was in assimilation rather than in transpiration. In spite of the micrometeorological feedback in all simulated circumstances, however, a considerable improvement of water use efficiency was found, varying between 1.3 for C_4 species to 1.7 for C_3 species. These results suggest that improvement of WUE is a more robust effect of CO_2 than its antitranspirant effect (Allen et al., 1985).

Crop Responses

During the growing season, several internal mechanisms operate in the plant modifying the initially observed effects of CO_2. In plants adapted to high CO_2, photosynthesis per unit leaf area is often smaller (Wong, 1979; Mortensen, 1983) than that of nonadapted plants (when measured under equal circumstances), but in soybean [*Glycine max* (L.) Merr.] stimulation of photosynthetic capacity has been observed (Valle et al., 1985; Campbell et al., 1988). When both grown and measured at a higher CO_2 concentration, leaves have generally a higher rate of photosynthesis. This is particularly true for N_2 fixing plants, which have nodules in their rooting system. The growth response of these plants to CO_2 tends to be particularly strong.

Starch accumulation (Ehret & Jolliffe, 1985) tends to cause some increase of leaf weight per unit leaf area. This rather passive response will not increase light interception, but the more active response of more leaf area formation by larger leaves or more tillers will further enhance the effect of increased CO_2 when considered at a crop level.

As shown in a review by Kimball (1983), responses at the single leaf level to CO_2 are carried over to crop yield and can be summarized by a mean 40% increase of dry matter for C_3 crops upon doubling of CO_2, and by 15% for C_4 crops.

A similar overall response for a C_3 crop was simulated by a fairly complicated model (Goudriaan et al., 1985), which considers the physiological mechanisms at the leaf level. More specifically, the model showed that the overall C response could be well-described by the following logarithmic equation (Fig. 8–4), at least in the domain of about 200 to 1000 μmol mol^{-1}:

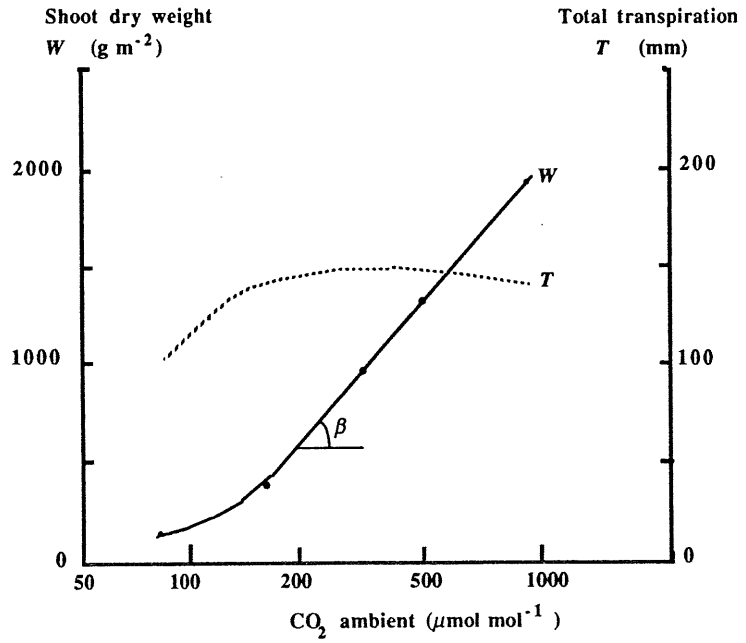

Fig. 8–4. Simulated total dry matter and whole season water consumption as affected by ambient CO_2, for a crop of Faba bean (Goudriaan et al., 1985).

$$\frac{W}{W_0} = 1 + \beta \ln\left(\frac{C}{C_0}\right) \qquad [1]$$

In this equation the subscript 0 stands for the reference situation, W for crop dry weight at the end of the season, and C for ambient CO_2 concentration. This equation is only indicative and has no physiological meaning, but it serves well to summarize many observations and simulation results. The response factor β of modelled crop dry weight was found to be 0.7 (see also Allen et al., 1987) when the increased C gain was invested again and used for increased tillering, increased leaf number, or increased leaf size. In this simulation run, total transpiration over the growing period did not decrease upon doubling of CO_2, in spite of stomatal closure, because the modeled increase of leaf area compensated for decreased leaf transpiration. Several experimental investigations have reported this type of stability of total crop transpiration (Jones et al. 1984; Kimball et al., 1983, 1984).

When no positive feedback on leaf area growth was assumed, the additional C was stored as starch in leaf or tuber, and the value of β was smaller, about 0.5. In this case the modeled cumulative transpiration did decrease in doubled CO_2.

INTERACTION WITH WATER SHORTAGE

The positive effect of CO_2, observed under good growing conditions, is fully maintained under water shortage. Gifford (1979) and Sionit et al. (1980) have shown that water relations, growth, and yield of wheat under water shortage can be considerably improved by raised ambient CO_2. Kimball et al. (1986) reported relative increases of cotton (*Gossypium hirsutum* L.) production ranging between 50 and 70% under doubled CO_2, in both optimal and limiting levels of water supply. Goudriaan and Bijlsma (1987) showed that WUE in Faba bean (*Vicia faba* L.) was improved by about 50% under doubled CO_2, for both normal and limited water supply. For a C_4 grass, however, Gifford and Morison (1985) found that growth stimulation by CO_2 began only under severe water stress.

In saline situations plants grow continually under osmotic stress. Schwarz and Gale (1984) found that the CO_2 effect on dry matter accumulation was equally strong or even more promounced in saline than in nonsaline situations, and that C_4 halophytes (plants that are salt-tolerant) responded as equally strongly as C_3 halophytes.

A major reason for the strong positive CO_2 effect under water stress, clearly, is the common physical pathway of water vapor and CO_2 through the stomatal pores. Another partial explanation can be found in better availability of assimilates for making osmotic adjustments and thereby maintaining turgor. These results are especially important for arid regions, where brackish or even saline situations are common.

When a limited stock of water is available, the plants may have adequate water most of the growing period. The water shortage only occurs by the time the soil has lost about 75% of its initial water content. The increased WUE as mentioned earlier will result in proportionally more biomass, but the amount of water left in the soil will be the same. However, if colimitation by nutrients or by crop development duration occurs, the increase in biomass will be too small to compensate for the decreased transpiration rate and the amount of soil water left after the growing period may increase.

INTERACTION WITH NUTRIENT SHORTAGE

Nutrient shortage tends to impose more strongly a limitation to crop growth than water shortage, without leaving much room for stimulation by CO_2. Increased starch accumulation in leaves grown under high CO_2 is responsible for a general increase in dry matter.

Phosphorus shortage was found to limit growth almost independently of CO_2 (350 and 700 μmol mol^{-1}) in a pot experiment (Goudriaan & de Ruiter, 1983). Also, the growth-limiting effect of K shortage was not alleviated by higher CO_2 (J. Goudriaan, 1985, unpublished data).

In open soil and perennial species a positive interaction may develop, by more intense rooting and increased soil weathering (Rosenberg, 1981). Norby et al. (1986) could not find a disappearance of the positive CO_2 effect, even at very low nutrient levels.

Nitrogen appears to be in an intermediate position, in allowing a small positive CO_2 effect, even under rather severe N shortage (Goudriaan & de Ruiter, 1983). In addition to starch accumulation, which generally lowers leaf nutrient contents, there is also a decrease in the carboxylation enzyme Rubisco, which contains up to 50% of leaf N. In accordance with this photosynthetic role of N, the N content in leaf tissue is lower for plants grown under high CO_2 than under low CO_2. In seed tissue, however, the C/N ratio is more stable (Kimball et al., 1986).

An intriguing question is how canopy transpiration is affected by CO_2 when plant growth is nutrient-limited. Lenssen (1986) showed that the transpiration reduction by higher CO_2 was still fully present under severe P limitation. This result is relevant for runoff from watersheds with naturally growing vegetation. Quite often these natural ecosystems are strongly nutrient-limited. When growth is not improved under increased CO_2, some increase of the water yields may be expected.

INTERACTION WITH CLIMATIC EFFECTS

Temperature and the Growing Season

In the absence of other limiting factors, temperature in cooler climate regions determines the length of the growing season, principally by its effects on the timing of developmental processes and on rates of expansion of leaves. Most processes of development and expansion (e.g., leaf expansion, flowering, grain filling) can be described by a linear increase of rate with temperature from a minimum threshold temperature to an optimum, and then a linear decrease to a maximum temperature limit, above which the process ceases (Monteith, 1981).

The implications of the temperature response for crop production depend on whether the growth form is *determinate* (as in cereals that have a discrete life cycle, ending when the crop is mature) or *indeterminate* (as in perennial grass or in potato, *Solanum tuberosum* L., which continues growing and forming yield as long as the temperature is above the minimum threshold). In determinate crops of temperate regions, higher temperatures decrease the time for which the canopy exists, and hence, decrease radiation interception and decrease potential yield. In contrast, higher temperatures *increase* the potential yield of indeterminate crops.

When higher temperatures are increased along with increased CO_2 concentrations, as in greenhouse effect scenarios, the two factors act in opposite directions for C_3 cereals. Squire and Unsworth (1988) used a mechanistic model of winter wheat growth to assess the impact of CO_2 and temperature on potential wheat yields in England. They assumed that water, nutrition, pests, and disease were not limiting factors.

When CO_2 concentration was doubled, but daily weather data from a typical year (1981) were used, the potential grain yield was 27% larger than in a control run at 340 μmol mol^{-1} CO_2 (11.5 and 9.0 Mg ha^{-1}, respec-

tively). The date of maturity was unchanged. When daily temperatures were increased by 3 °C *and* CO_2 was doubled, more rapid development of the crop shortened the growing season, and the potential grain yield (10.4 Mg ha^{-1}) was only 15% larger than in the control, but maturity occurred 30 d earlier. A combination of +4.5 °C and doubled CO_2 resulted in the temperature and CO_2 factors almost cancelling out, so that the potential grain yield (9.7 Mg ha^{-1}) was only 8% larger than the control. Maturity was 40 d earlier than in 1981 conditions.

On the other hand, in some conditions also in determinate species a positive interaction with temperature exists. Maize in northwestern Europe does not reach maturation, but it is used as a silage crop instead. Because its fodder value is largely determined by the fraction of cobs, even when not mature, a longer growing season is highly profitable. Moreover, in these cool regions maize usually grows below its optimal temperature for photosynthesis.

In most regions in North America (Rosenzweig, 1985), and also in southern Europe, increased temperature would lead to losses of crop yield; the same conclusion applies to the tropical and subtropical regions of the world. Moreover, especially in the tropics, agriculture tends to suffer from nutrient shortage, which further impairs the potential to utilize the beneficial direct effects of increased CO_2.

Negative compensatory effects due to water shortage in midsummer may still occur. Also, pests and diseases may become more serious, because more time will be available for them to generate larger populations during the growing season, and because of greater survival through the winter.

Other Climatic Factors

Other climatic factors such as precipitation and radiation are no less important than temperature (Rosenberg et al., 1990). Unfortunately, there is even less certainty about the way they will change than there is for temperature. Crop growth models show that the potential productivity is closely related to incoming radiation during the growing season, but the GCM's are not able to produce reliable predictions on this point yet. Therefore, the possible impact of radiation change is usually ignored, in spite of its potential importance.

For precipitation, the currently available figure is that the mean global precipitation will increase by 7 to 15% (Wilson & Mitchell, 1987). Some regional specification can be obtained from maps such as produced by Schlesinger and Mitchell (1985). A model for wheat and rice (*Oryza sativa* L.) that included both the climatic (temperature and precipitation) effects and the physiological effects of doubled CO_2 (van Diepen et al., 1987), predicted potential crop yields to increase by 10 to 50% for some sites in Europe and Asia. The mean GCM scenarios were superimposed on current weather, retaining current variability. The resulting yield variability was not increased, except in the Mediterranean zones.

In another simulation study for crop yields in the USA, Curry et al. (1988) used climate scenarios based on GCM studies with the GISS model

and GFDL models (Taylor & MacCracken, Chapter 1, this book). However, the precipitation scenarios from these models were quite different, and also showed, month by month, extremely uneven precipitation changes. Further climate study will be needed to confirm if such extreme changes are realistic.

SOME HYDROLOGICAL CONSIDERATIONS

A Simple Equation for Runoff

River runoff is one of the major factors for the availability of water resources (da Cunha, 1988). Runoff is precipitation that has not been either evaporated or stored in the soil. Collected over an entire river catchment area, it gives rise to the river discharge. Because river discharge is the result of spatially heterogeneous and time-varying contributions from subcatchment areas, complicated models are required for its complete description (Gleick, 1986, 1987).

Here a rudimentary analysis will be given based on a few simple equations. Averaged over the annual cycle, soil storage can be neglected and the runoff, R, is simply the difference between precipitation, P, and actual evapotranspiration, E:

$$R = P - E \qquad [2a]$$

The type of vegetation can have a considerable effect on E, even under the same climatic conditions (Dickinson & Henderson-Sellers, 1988). For example, Dolman and Nonhebel (1988) showed that a spruce (*Picea* sp.) forest loses much more water than an oak (*Guercus* sp.) forest due to direct evaporation of intercepted water. In fact, for long-term studies the change of vegetation type along with climate should also be taken into account. This problem can be partly solved by using an equation that includes covariation of vegetation with climate. For that purpose we use the following simple, old empirical equation for actual annual evapotranspiration, E, based on annual precipitation, P, and potential evapotranspiration E_p. This equation goes back to Oldekop (1911) (Dooge, 1988):

$$E = E_p \tanh (P/E_p) \qquad [2b]$$

This equation does not include the water holding capacity of the soil nor the effect of vegetation on any other surface parameterizations. It does, however, follow the basic physical requirements that E approaches to P for very low P/E_p on one hand, and to E_p for very high P/E_p on the other. The equation also performs well when P and E_p are of the same order (Table 8-2).

As shown in Table 8-2, mean runoff is well predicted. In the polders in the Netherlands (de Vries, 1980), not only precipitation (750 mm yr^{-1}), but also seepage water and inlet water (180 mm yr^{-1}), contribute to the

Table 8-2. Comparison of the equation $R = P - E_p \tanh(P/E_p)$ and observed data for a few regions.

Region	P	E_p	$R_{predicted}$	$R_{observed}$
			mm yr^{-1}	
Eastern USA (Schaake, 1990)	1140	890	378	355-410
Upper Colorado (Revelle & Waggoner, 1983)	350	450	57	53
Rhine catchment (Thran & Broekhuizen, 1965)	800	600	278	280
Polders in Holland (de Vries, 1980)	750	600	241	440
With seepage and inlet	930	600	382	440

positive side of the water balance, in total 930 mm yr^{-1}. Potential evaporation is 600 mm yr^{-1}, so that R is predicted to be 382 mm yr^{-1}, close to the 440 mm yr^{-1} that is pumped out in reality.

The behavior of R, based on Eq. [2a] and [2b], is graphed in Fig. 8-5 by isolines for R as a function of P and E_p. Two widely different locations are indicated in the graph, an "R" for the river Rhine catchment area, and a "C" for the Colorado River catchment area. The major river in northwestern Europe, the river Rhine, has a catchment area of about 220 000 km^2, and a mean discharge of 2000 m^3 s^{-1}. According to the maps compiled by Thran and Broekhuizen (1965), the mean precipitation over the catchment area is 800 mm yr^{-1} and the mean potential evaporation is 600 mm yr^{-1}, so that Eq. [2] predicts a mean runoff of 278 mm yr^{-1}. This leads

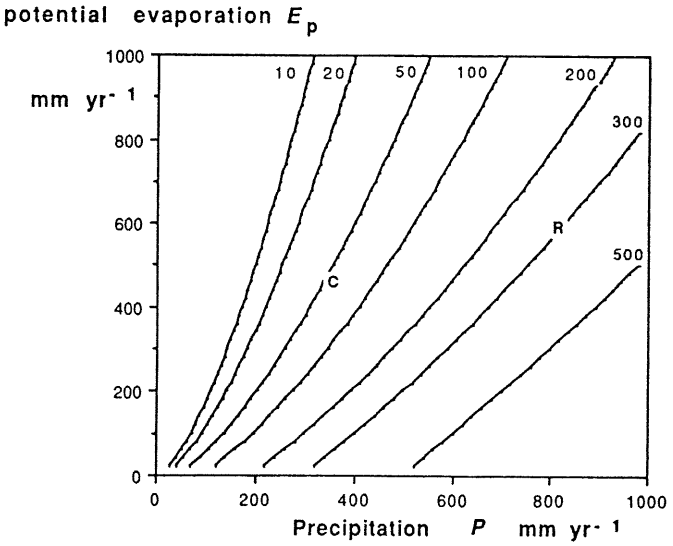

Fig. 8-5. Isolines of equal runoff as a function of precipitation, P, and potential evaporation, E_p, calculated with Eq. [2]; C and R characterize the catchment areas of the Upper Colorado and the Rhine River, respectively.

to a predicted river discharge of 1940 $m^3 s^{-1}$, in excellent agreement with the data. For the Colorado River we used the publication of Revelle and Waggoner (1983), who give a P of 350 mm yr^{-1} and an E_p of 450 mm yr^{-1}, based on Langbein et al. (1949). Equation [2] then gives 57 mm yr^{-1} as discharge, which compares very well with the 53 mm yr^{-1} mentioned by Revelle and Waggoner.

This equation is useful because of its simplicity, enabling a quick assessment of the sensitivities of river discharge for changes in precipitation and potential evaporation. According to the GCM studies, the expected global warming will be accompanied by an increased hydrological cycle. Averaged over the whole globe, P and E_p will increase by 7 to 15% upon doubling of atmospheric CO_2. A robust first-order conclusion is that the runoff ratio R/P will not alter if P and E_p increase by the same relative fraction. The mean runoff R itself will then also increase by about 7 to 15%. Regionally, of course, P and E_p may change in a different way. If just P and not E_p increases, runoff will increase much more than proportionally, and vice versa. According to Eq. [2], the relative sensitivity of R to P, $(\Delta R/R)/(\Delta P/P)$, is as high as 3 in very dry regions ($P/E_p \ll 1$), and drops to about 2.4 at $P/E_p = 1$ and 1.8 at $P/E_p = 2$. If, on the other hand, only E_p increases, R to E_p will be diminished with a relative sensitivity, $(\Delta R/R)/(\Delta E_p/E_p)$, of -2 in very dry regions, -1.4 in moderately humid zones ($P/E_p = 1$), and -0.8 in very humid conditions ($P/E_p = 2$).

In most temperate climates, precipitation and potential evaporation are of similar magnitude. According to Eq. [2] the runoff is then about 25% of the precipitation, and the relative sensitivities of R to P and E_p are 2.4 and -1.4, respectively.

Climate Change and Annual Precipitation/Potential Evaporation Ratio

The simplest explanation for the contrast of summer dryness and winter wetness, at least in temperate and mediterranean climates of the world, is the following. In winter the oceans are still relatively warm and can give moisture to the air above them. This humid air spreads out and the relatively cold continents receive a surplus of winter precipitation, especially at their margins. Because of the low temperatures, almost no moisture is returned to the air, so the center regions of the continents stay cold and dry. In summer, on the other hand, the surface temperature of the sea lags behind that of the land. The precipitation surplus at the continents disappears, but now there is a large evapotranspiration from the land masses. In combination with the large moisture-carrying capacity of the warm air, precipitation is now supplied to the continental center regions as well.

Clearly, dryness and temperature are highly correlated when they are both followed over the seasons. Why, then, should there not be more dryness when temperature rises due to the greenhouse effect? There is no reason to assume that the annual temperature cycle, and in particular the phase lag between sea and land, will become more extreme. The greenhouse warming will be so slow that, to a first approximation, both cycles at land and sea

will go up together. Therefore, a generally increased dryness is not to be expected. Temporarily the sea temperature may show some lag, but with a magnitude that is likely to be negligible in comparison to the annual cycle.

This is not to say that locally no changes in climate can occur, but even then it should be kept in mind that the geographical distribution of aridity patterns is largely governed by mountain ranges and by cold and warm ocean currents. These currents of course may shift, which poses the largest danger. For northwestern Europe the Gulf Stream is vital, and it would be a disaster if it disappeared or even changed its course. The importance of sea surface temperature was recently confirmed by Palmer and Brankovic (1989).

Direct Carbon Dioxide Effects and Annual Precipitation/Potential Evaporation Ratio

In extremely wet climates, the evapotranspiration will not be affected by CO_2. Vegetation and soil are wet all the time, and almost all evaporation is direct evaporation of intercepted water, in which stomatal opening plays no role. But also in extremely dry climates the role of vegetation is negligible, and runoff is largely governed by excess water flowing from the bare ground after an occasional storm. A better WUE of vegetation will help the vegetation survive or increase its biomass, but the water yield from the catchment area will not rise. Conceivably, an increase in vegetation could even reduce water yield in these arid regions by reducing the ease with which water runs off after the occasional rains.

In the important intermediate situation where P and E_p are of similar magnitude, some reduction of actual transpiration may occur. The results discussed earlier, however, indicate an increased leaf area will compensate for decreases in stomatal opening. A purely empirical equation such as Eq. [2b] cannot account for such effects, and detailed mechanistic models will be necessary. Our expectation is, however, that such effects will be small, and that changes in type of land use will be much more important.

CONCLUSIONS

Implications for Global Agriculture

A rather detailed simulation experiment by Wilks (1988), using a physiological process-based simulation model for cereal growth, in combination with GCM based information on climate change in a double-CO_2 world indicated that for the USA Corn Belt the expectation for crop yield is not dominantly negative. Both positive and negative effects for wheat and corn (*Zea mays* L.) were predicted, ranging between -40% and $+80\%$. The direct physiological effects of CO_2 on photosynthesis and stomatal opening were not included, however. Similarly, Parry et al. (1988) and Rosenzweig (1985) did not consider the direct effects of CO_2, and it seems safe to consider these results as "worst case" scenarios. As explained, the direct effects of CO_2

for crop production are generally beneficial and can be added to the indirect climatic effects. Direct and indirect effects together will probably show a predominantly positive picture.

Over the period 1959 to 1986, almost 30 yr, the world average grain yield per unit area has increased from about 1400 kg ha^{-1} to about 2600 kg ha^{-1} (FAO, 1987). This near-doubling is the result of a continued annual relative growth rate of about 2.3% per year. At the same time, atmospheric CO_2 has risen from 315 to about 345 μmol mol^{-1}, at an average relative rate of about 0.34% yr^{-1}. When plotted together the correlation is almost perfect (Fig. 8-6). It would be very unwise indeed to draw any conclusions from this graph as far as cause and effect are concerned. Rather, it brings us to some interesting considerations.

It shows that the relative growth rate of cereal production (on an area basis) has been seven times as large as that of atmospheric CO_2. Even under optimal conditions for growth, the socalled β factor of CO_2 will rarely exceed the value of 0.5, which means that at most 1/14 of the actual increases in crop production can be reasonably ascribed to increasing atmospheric CO_2. Is this much? It is indeed, if one considers it as a free premium, on which we can reckon in the foreseeable future. It is not large, however, if it is compared with the human dynamics in the agricultural technology. In fact, its relatively small impact confirms the point of view of those who consider the climatic change issue as minor when compared with other opportunities and dangers of a man-made nature. The slowness of the steady drift

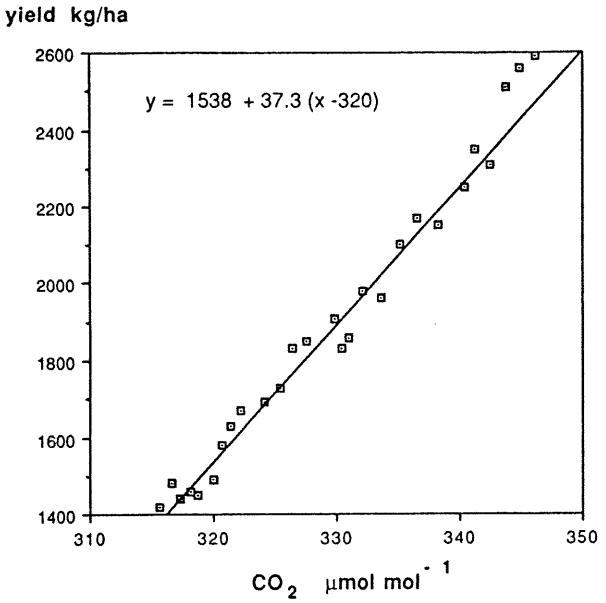

Fig. 8-6. World average grain yields over the period 1959 to 1986 (kindly supplied by H. van Heemst at CABO, Wageningen from FAO production yearbooks) vs. atmospheric CO_2, measured at Mauna Loa, HI.

of the environment permits ample time for adaptation, even for time-demanding activities such as plant breeding (Wittwer, 1980).

There is, however, also a danger in this point of view, namely that it is too general. There may be parts of the world where agriculture may be even completely pushed out of its borders of existence, most literally by sea-level rise, but also by deterioration of already extreme climatic conditions.

REFERENCES

Allen, L.H., K.J. Boote, J.W. Jones, P.H. Jones, R.R. Valle, B. Acock, H.H. Rogers, and R.C. Dahlman. 1987. Response of vegetation to rising carbon dioxide: Photosynthesis, biomass, and seed yield of soybean. Global Biogeochem. Cycles 1:1-14.

Allen, L.H., P. Jones, and J.W. Jones. 1985. Rising atmospheric CO_2 and evapotranspiration. p. 13-27. *In* Advances in evapotranspiration ASAE Publ. 14-85. ASAE, St. Joseph, MI.

Campbell, W.J., L.H. Allen, and G. Bowes. 1988. Effects of CO_2 concentration on Rubisco activity, amount, and photosynthesis in soybean leaves. Plant Physiol. 88:1310-1316.

Chen, J. 1984. Uncoupled multi-layer model for the transfer of sensible and latent heat flux densities from vegetation. Boundary-Layer Meteorol. 28:213-226.

Cure, J.D., and B. Acock. 1986. Crop responses to carbon dioxide doubling: A literature survey. Agric. For. Meterol. 38:127-145.

Curry, R.B., R.M. Peart, J.W. Jones, K.J. Boote, and L.H. Allen, Jr. 1988. Simulation as a tool for analyzing crop response to climate change. ASAE Pap. 88-7512. ASAE, St. Joseph, MI.

da Cunha, L.V. 1988. Climatic changes and water resources development. p. 639-660. *In* A. Berger et al. (ed.) Climate and geo-sciences. NATO ASI Ser. C. Vol 285. Kluwer Academic Publ., Dordrecht, Netherlands.

de Vries, J.J. 1980. Hydrologie van Nedereland. Rodopi, Amsterdam, Netherlands. (in Dutch).

Dickinson, R.E., and A. Henderson-Sellers. 1988. Modelling tropical deforestation: A study of GCM land-surface parameterizations. Q. J. R. Meteorol. Soc. 114:439-462.

Dolman, A.J., and S. Nonhebel. 1988. Modelling forest water consumption in The Netherlands. Agric. Water Manage. 14:413-422.

Dooge, J.C.I. 1988. The role of the hydrological cycle in climate. p. 355-366. *In* A. Berger et al. (ed.) Climate and geo-sciences. NATO ASI Ser. C. Vol. 285. Kluwer Academic Publ., Dordrecht, Netherlands.

Ehret, D.L., and P.A. Jolliffe. 1985. Photosynthetic carbon dioxide exchange of bean plants grown at elevated carbon dioxide concentration. Can. J. Bot. 63:2026-2030.

Enoch, H.Z., and B.A. Kimball. 1986. CO_2 enrichment of greenhouse crops. Vol. 1 and 2. CRC Press, Boca Raton, FL.

Farquhar, G.D., and S. von Caemmerer. 1983. Modelling of photosynthetic response to environmental conditions, encyclopedia of plant physiology. Vol. 12B. Springer-Verlag, New York.

Food and Agriculture Organization of the United Nations. 1987. FAO production yearbook. FAO, Rome, Italy.

Gaastra, P. 1962. Photosynthesis of leaves and field crops. Neth. J. Agric. Sci. 10:311-324.

Gezondheidsraad. 1983. Part One report on CO_2 problem (English translation). Recommendation to the Ministers of Public Health and of the Physical Environment issued by the Health Council of the Netherlands. Health Council, The Hague, Netherlands.

Gezondheidsraad. 1987. CO_2 problem, scientific opinions and impacts on society (English translation). Second advice and final report. Health Council, The Hague, Netherlands.

Gifford, R.M. 1979. Growth and yield of carbon dioxide-enriched wheat under water-limited conditions. Aust. J. Plant Physiol. 6:367-378.

Gifford, R.M., and J.I.L. Morison. 1985. Photosynthesis, water use and growth of a C_4-grass stand at high CO_2-concentration. Photosynth. Res. 7:77-90.

Gleick, P.H. 1986. Methods for evaluating the regional hydrologic impacts of global climatic changes. J. Hydrol. 88:97-116.

Gleick, P.H. 1987. Regional hydrologic consequences of increases in atmospheric CO_2 and other trace gases. Clim. Change 10:137–161.

Goudriaan, J. 1977. Crop micrometeorology: A simulation study. Simulation Monographs. Pudoc, Wageningen, Netherlands.

Goudriaan, J., and R.J. Bijlsma. 1987. Effect of CO_2-enrichment on growth of faba beans at two levels of water supply. Neth. J. Agric. Sci. 35:189–191.

Goudriaan, J., and H.E. de Ruiter. 1983. Plant growth in response to CO_2-enrichment, at two levels of nitrogen and phosphorus supply. Neth. J. Agric. Sci. 31:157–169.

Goudriaan, J., and H. van Keulen. 1979. The direct and indirect effects of nitrogen shortage on photosynthesis and transpiration in maize and sunflower. Neth. J. Agric. Sci. 27:227–234.

Goudriaan, J., and H.H. van Laar. 1978. Relations between leaf resistance, CO_2 concentration and CO_2 assimilation in maize, beans, lalang grass and sunflower. Photosynthetica 12:241–249.

Goudriaan, J., H.H. van Laar, H. van Keulen, and W. Louwerse. 1985. Photosynthesis, CO_2 and plant production. p. 107–122. *In* W. Day and R.K. Atkin (ed.) Wheat growth and modelling. NATO ASI Ser. A: Life Sciences. Vol. 86. Plenum Publishing, New York.

Jarvis, P.G., and K.G. McNaughton. 1986. Stomatal control of transpiration: Scaling up from leaf to region. p. 1–49. *In* Advances in ecological research. Vol. 15. Academic Press, New York.

Jones, P., L.H. Allen, K.J. Boote, and W.J. Campbell. 1984. Soybean canopy growth, photosynthesis, and transpiration responses to whole-season carbon dioxide enrichment. Agron. J. 76:633–637.

Kimball, B.A. 1983. Carbon dioxide and agricultural yield: An assemblage and analysis of 430 prior observations. Agron. J. 75:779–788.

Kimball, B.A., J.R. Mauney, G. Guinn, F.S. Nakayama, P.J. Pinter, K.L. Clawson, S.B. Idso, G.D. Butler, Jr., and J.W. Radin. 1984. Effects of increasing atmospheric CO_2 on the yield and water use of crops. *In* Response of vegetation to carbon dioxide. Ser. 023. U.S. Dep. of Energy, and USDA-ARS, Washington, DC.

Kimball, B.A., J.R. Mauney, G. Guinn, F.S. Nakayama, P.J. Pinter, K.L. Clawson, R.J. Reginato, and S.B. Idso. 1983. Effects of increasing atmospheric CO_2 on the yield and water use of crops. *In* Response of vegetation to carbon dioxide. Ser. 021. U.S. Dep. of Energy and USDA-ARS, Washington, DC.

Kimball, B.A., J.R. Mauney, J.W. Radin, F.S. Nakayama, S.B. Idso, D.L. Hendrix, D.H. Akey, S.G. Allen, M.G. Anderson, and W. Hartung. 1986. Effects of increasing atmospheric CO_2 on the growth, water relations, and physiology of plants grown under optimal and limiting levels of water and nitrogen. *In* Response of vegetation to carbon dioxide. Ser. 039. U.S. Dep. of Energy and USDA-ARS, Washington, DC.

Langbein, W.B., et al. 1949. Annual runoff in the United States. USGS Circ. 5. U.S. Dep. of the Interior, Washington, DC.

Lemon, E.R. (ed.). 1983. CO_2 and plants. AAAS Selected Symp. 84. Westview Press, Boulder, CO.

Lenssen, G.M. 1986. De invloed van CO_2 in combinatie met fosfaatgerbrek op de groei en de transpiratie van tarwe. M.Sc. thesis. Agricultural Univ., Wageningen, Netherlands (in Dutch).

Louwerse, W. 1980. Effects of CO_2 concentration and irradiance on the stomatal behaviour of maize, barley and sunflower plants in the field. Plant Cell Environ. 3:391–398.

Monteith, J.L. 1981. Climate variation and growth of crops. Q. J. R. Meterol. Soc. 107:749–774.

Morison, J.I.L. 1987. Intercellular CO_2 concentration and stomatal response to CO_2. *In* E. Zeiger et al. (ed.) Stomatal function. Stanford Univ. Press, Stanford, CA.

Mortensen, L.M. 1983. Growth responses of some greenhouse plants to environment: X. Long-term effect of CO_2 enrichment on photosynthesis, photorespiration, carbohydrate content and growth of *Chrysanthemum morifolium* Ramat. Sci. Rep. 272. Agric. Univ. of Norway. Vol. 62. The Agric. Univ. of Norway, Ås, Norway.

Nederhoff, E.M., and A.M. van Uffelen. 1988. Effects of continuous and intermittent carbon dioxide enrichment on fruit set and yield of sweet pepper (*Capsicum annuum* L.). Neth. J. Agric. Sci. 36:209–217.

Norby, R.J., E.G. O'Neill, and R.J. Luxmoore. 1986. Effects of atmospheric CO_2 enrichment on the growth and mineral nutrition of *Quercus alba* seedlings in nutrient-poor soil. Plant Physiol. 82:83–89.

Oldekop, E.M. 1911. On evaporation from the surface of river basins. Sbornik. trudov, ispolnevykh studentami pri Iurievskoj observatorii (Tartu). Univ. of Tartu, Estonia.

Palmer, T.N., and C. Brankovic. 1989. The 1988 U.S. drought linked to anomalous sea surface temperature. Nature (London) 339:54–57.

Parry, M.L., T.R. Carter, and N.T. Konijn. 1988. The impact of climatic variations on agriculture. Vol. 1: Assessments in cool temperate and cold regions. Vol. 2: Assessments in semi-arid regions. Kluwer, Dordrecht, Netherlands.

Pearcy, R.W., and J. Ehleringer. 1984. Comparative ecophysiology of C_3 and C_4 plants. Plant Cell Environ. 7:1–13.

Ramanathan, V., R.D. Cess, E.F. Harrison, P. Minnis, B.R. Barkstrom, E. Ahmad, and D. Hartmann. 1989. Cloud-radiative forcing and climate: Results from the Earth radiation budget experiment. Science (Washington, DC) 243:57–63.

Raschke, K. 1975. Stomatal action. Annu. Rev. Plant Physiol. 26:309–340.

Revelle, R.R., and P.E. Waggoner. 1983. Effects of a carbon dioxide-induced climatic change on water supplies in the Western United States. *In* Changing climate. Rep. of the Carbon Dioxide Assessment Committee. National Academy Press, Washington DC.

Rosenberg, N.J. 1981. The increasing CO_2-concentration in the atmosphere and its implication on agricultural productivity. Clim. Change 3:265–279.

Rosenberg, N.J., B.A. Kimball, Ph. Martin, and C.F. Cooper. 1990. From climate and CO_2 enrichment to evapotranspiration. p. 151–175 *In* P.E. Waggoner (ed.) Climate change and U.S. water resources. John Wiley & Sons, New York.

Rosenzweig, C. 1985. Potential CO_2-induced climate effects on North American wheat-producing regions. Clim. Change 7:367–389.

Schaake, J.C. 1990. From climate to flow. p. 176. *In* P.E. Waggoner (ed.) Climate change and U.S. water resources. John Wiley & Sons, New York.

Schlesinger, M.E., and J.F.B. Mitchell. 1985. Model projections of the equilibrium climatic response to increased carbon dioxide. *In* M.C. MacCracken and F.M. Luther (ed.) The potential climatic effects of increasing carbon dioxide. DOE/ER-0237. U.S. Dep. of Energy, Washington, DC. Available from NTIS, Springfield, VA.

Schwarz, M., and J. Gale. 1984. Growth response to salinity at high levels of carbon dioxide. J. Exp. Bot. 35:193–196.

Sionit, N., N. Hellmers, and B.R. Strain. 1980. Growth and yield of wheat under CO_2-enrichment and water stress. Crop Sci. 20:456–458.

Squire, G.R., and M.H. Unsworth. 1988. Effects of CO_2 and climatic change on agriculture, 1988. Rep. to the UK Dep. of Environ. Univ. of Nottingham, UK.

Strain, B.R., and J.D. Cure. 1985. Direct effects of increasing carbon dioxide on vegetation. DOE/ER-0238. U.S. Dep. of Energy, Washington, DC. Available from NTIS, Springfield, VA.

Thran, P., and S. Broekhuizen. 1965. Agro-ecological atlas of cereal growing in Europe. Vol. I. Agro-climatic atlas of Europe. Elsevier Science Publishing, New York.

Valle, R., J.W. Mishoe, W.J. Campbell, J.W. Jones, and L.H. Allen. 1985. Photosynthetic responses of 'Bragg' soybean leaves adapted to different CO_2 environments. Crop Sci. 25:333–339.

van Diepen, C.A., H. van Keulen, F.W.T. Penning de Vries, I.G.A.M. Noy, and J. Goudriaan. 1987. Simulated variability of wheat and rice yields in current weather conditions and in future weather when ambient CO_2 has doubled. Simulation Rep. CABO-TT Nr 14. CABO, Wageningen, Netherlands.

Wilks, D.S. 1988. Estimating the consequences of CO_2-induced climatic change on North American grain agriculture using General Circulation Model information. Clim. Change 13:19–42.

Wilson, C.A., and J.F.B. Mitchell. 1987. A doubled CO_2 climate sensitivity experiment with a global climate model including a simple ocean. J. Geophys. Res. 92:13 315–13 343.

Wittwer, S.H. 1980. Carbon dioxide and climatic change: An agricultural perspective. J. Soil Water Conserv. 35:116–120.

Wittwer, S.H., and W. Robb. 1964. Carbon dioxide enrichment of greenhouse atmospheres for food crop production. Econ. Bot. 18:34–56.

Wong, S.C. 1979. Elevated atmospheric partial pressure of CO_2 and plant growth. I. Interactions of nitrogen nutrition and photosynthetic capacity in C_3 and C_4 plants. Oecologia 44:68–74.